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VARIATION IN *HOYA AUSTRALIS* R. BR. EX TRAILL (ASCLEPIADACEAE)

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Summary

***Hoya australis* R. Br. ex Traill is a highly variable taxon that occurs in Australia, Papuasia and Melanesia. Five subspecies are recognised within *H. australis*, defined by vegetative characters and floral phenology. *H. australis* subsp. *oramicola* is newly described and the new combinations *H. australis* subsp. *tenuipes* (*H. oligotricha* subsp. *tenuipes* K. Hill) and *H. australis* subsp. *rupicola* (*H. rupicola* K. Hill) are made.**

Introduction

As noted by Liddle (1986) and Hill (1988), *H. australis* is an exceptionally variable taxon with a wide distribution in Australia, Papuasia and Melanesia. The recent account of the complex within Australia by Hill (1988) is deficient in several regards, firstly in that it does not recognise all of the variants that do occur, secondly in that it recognises 'variants' that do not occur, thirdly in the use of several characters primarily of indumentum that are of little use in taxon delimitation at the specific level, fourthly in the omission of several diagnostic characters that are obvious with live material and fifthly in the incorrect indication of the location of several types.

The *H. australis* complex encompasses a number of previously described taxa, namely *Gymnema recurvifolium* Blume, *Hoya dalrympleana* F. Muell., *H. bicarinata* Gray, *H. keysii* Bailey, *H. sanae* ("sana") Bailey, *H. papillantha* Schumann, *H. pubescens* Reinecke, *H. lactea* S. Moore, *H. oligotricha* K. Hill, *H. oligotricha* subsp. *tenuipes* K. Hill and *H. rupicola* K. Hill. These taxa exhibit a wide range of vegetative forms but are relatively uniform in terms of floral morphology. In this paper we attempt to reassess the wide variation in the group throughout its entire range and to define taxa based on discontinuities in morphology, ecological separation and phenological differentiation. As with other taxa of the genus, field observations and the study of live or pickled material is essential, as both floral and vegetative characters of these plants become considerably distorted and difficult to interpret once material is pressed and dried. Our taxonomic decisions are based on extensive field studies in Australia and the examination of a large number of plants of known origin under uniform conditions of cultivation.

Materials and Methods

Field studies in Queensland and the Northern Territory were undertaken by us from around 1978 onwards. A large number of plants from wild populations were cultivated both at Emerald Creek, Mareeba and Brisbane during this period.

Flowering material of these collections was pickled in 70% alcohol, glycerol and water and subsequently used for measurement of floral characters. Vegetative characters were determined from live plants that were flowering or that had previously flowered. It should be noted that since plants of this complex will only flower in bright light, measurements of vegetative characters were obtained from plants grown under these conditions. Plants grown in dense shade tend to have much thinner, larger leaves (cf. Adams *et al.* 1988, and our observations) and do not flower.

In the taxonomic section we have cited representative collections under the separate taxa, mainly to demonstrate the geographical distribution of each subspecies. For Australia these are collections that have been examined in the field, subsequently cultivated and represented, at least in BRI, both by dried and spirit material. A full list of collections seen is given in **Appendix 1**. The maps show Australian distributions only, as we have not seen comprehensive herbarium material of these plants from Papuasia and Melanesia, nor have we conducted field studies in these regions.

The following characters were measured on 142 clones of known wild origin. The number of samples for each clone is indicated in [ ] brackets.

(1) habit: (a) twining, (b) erect or scrambling but not twining. [1].

(2) leaf type: (a) very succulent, (b) fleshy to succulent (c) coriaceous. [1].
Note: "very succulent" denotes leaf thickness of 2.5–3.5 mm, "fleshy to succulent" denotes leaf thickness of 1.2–1.6 mm; coriaceous denotes leaf thickness < 1.2 mm (cf. Forster 1990b).

(3) leaf margin: (a) not recurved, (b) strongly recurved. [1].

(4) leaf venation: (a) prominent, (b) obscure. [1].

(5) indumentum: (a) absent, (b) scattered, (c) sparse (d) dense. [10].
Note: Hill (1988) placed much emphasis on the orientation of indumentum in definition of taxa in the group. We observed that this could be variable both within and between populations and have not used it as a character. Indumentum cover is defined using the system developed by Hewson (1988), except that we use the term 'scattered' instead of 'isolated'.

(6) extrafloral nectaries on lamina: (a) present, (b) absent. [10].

(7) lamina length and width. [10].

(8) flower diameter. [5].

(9) pedicel length and width. [5].

(10) sepal length and width. [5].

(11) corolla lobe length and width. [5].

(12) staminal corona diameter. [5].

(13) individual staminal corona lobe length. [5].

(14) individual staminal corona lobe width. [5].

(15) length of slit between anther wing. [5].

(16) pollinium length and width. [5].

(17) corpusculum length and width. [5].

(18) caudicle length and width. [5].

Where possible 5 flowers from the same inflorescence were scored separately for characters 8–18, but where less than 5 flowers were present, scoring was increased on individual flowers.

Results

Plants could be consistently allocated to one of five groups on a number of characters of habit and leaf morphology. These characters are summarised in **Table 1.**

Table 1. Allocation of clones of *H. australis* complex into 5 groups on the basis of plant habit and leaf morphology characters that exhibit variation

Character	Group				
	1	2	3	4	5
(1) **habit:** (a) twining, (b) erect or scrambling, but not twining	a	a	b	a	a
(2) **leaf type:** (a) very succulent (b) fleshy to succulent, (c) coriaceous	b	c	a	b	b
(3) **leaf margin:** (a) not recurved, (b) strongly recurved	a	a	a	b	b
(4) **leaf venation:** (a) prominent (b) obscure	b	b	b	a	b
(5) **extrafloral nectaries on lamina:** (a) present, (b) absent	a	a	b	ab	b

Plants could not be consistently allocated into groups on the basis of lamina indumentum cover, lamina length and width or the ratio of the latter two. Plants of groups 3 and 4 (**Table 1**) tend to have dense indumentum on both lamina surfaces, but particularly on the adaxial surface. Plants of group 1 tend to have sparse to dense indumentum, often on both lamina surfaces, but also quite commonly only on the adaxial surface. Plants of group 2 are glabrous or have scattered to sparse indumentum on the lamina surfaces. Leaf length and width varies considerably across all groups, although there was a slight tendency for plants of group 3 to have more lanceolate leaves than those of the other groups (**Fig. 1**).

Flower shape was consistent throughout the clones examined. The number of flowers per inflorescence and pedicel length appeared to be dependent on individual growing conditions and could vary from inflorescence to inflorescence or from year to year on the same plant. Flower size was extremely variable with most noticeable variation being in the corolla lobe length and width (**Fig. 2**) and pollinium length and width (**Fig. 3**). Very small flowers tended to have small coronas and small pollinaria, whereas very large flowers tended to have large coronas and large pollinaria. There was continuous variation in all floral characters between all groups defined on vegetative characters.

Plants of the five groups defined on habit and leaf morphology (**Table 1**) tend to have, but not exclusively so, discrete flowering periods in Australia (Group 1: March–May; Group 2: September–October, rarely March–May; Groups 3 & 5: January–March; Group 4: May–July) and also occur in different habitat types. Plants of groups 1 and 2 occur over much the same geographical range in north Queensland but are always ecologically discrete, although at times the physical distance between them may be small. Plants of groups 1 and 4 are generally found in different areas, but both occur in close proximity in the Glennie Tableland area on Cape York Peninsula.

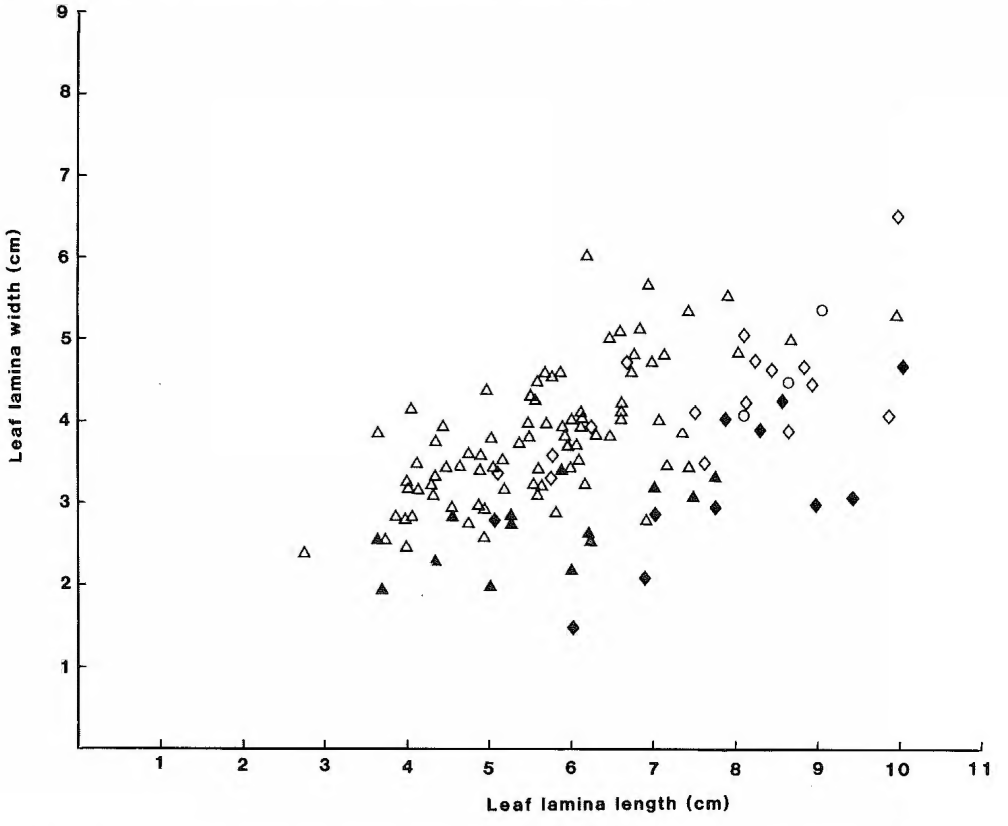

Fig. 1. Leaf lamina length versus leaf lamina width in *Hoya australis*. △ Group 1 (subsp. *australis*); ▲ Group 2 (subsp. *sanae*); ◆ Group 3 (subsp. *rupicola*); ◇ Group 4 (subsp. *tenuipes*); ○ Group 5 (subsp. *oramicola*.

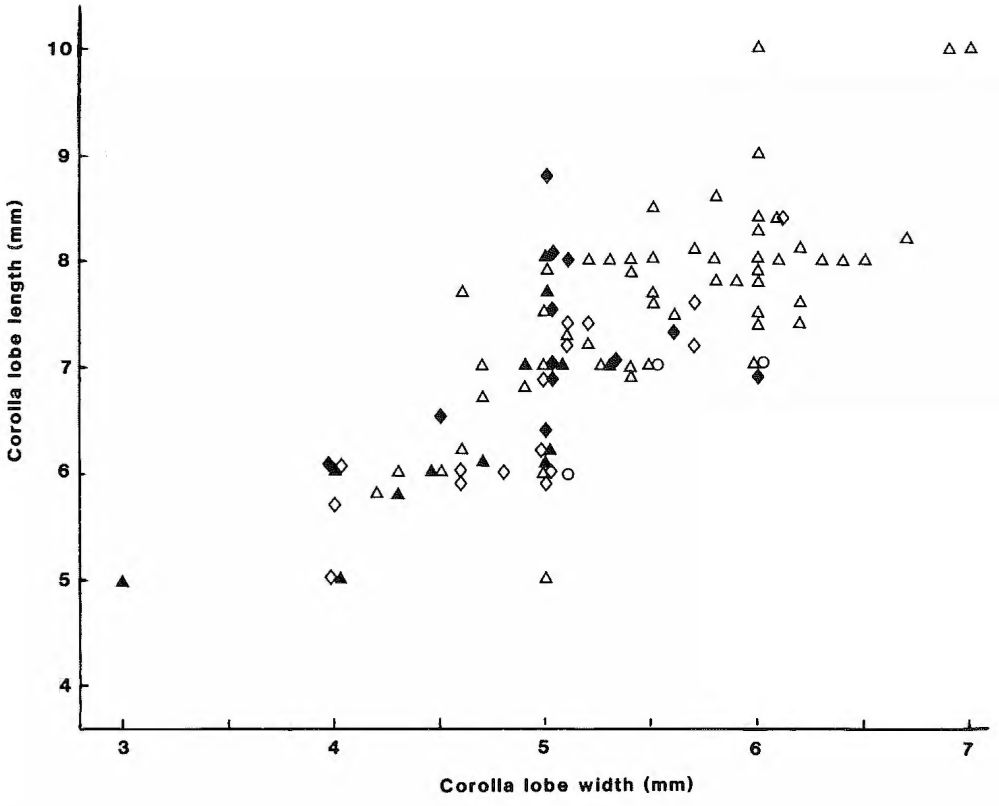

Fig. 2. Corolla lobe length versus corolla lobe width in *Hoya australis*. △ Group 1 (subsp. *australis*); ▲ Group 2 (subsp. *sanae*); ◆ Group 3 (subsp. *rupicola*); ◇ Group 4 (subsp. *tenuipes*); ○ Group 5 (subsp. *oramicola*.

Discussion

In the genus *Hoya* (Forster & Liddle 1990; Rintz 1978) and elsewhere in the family Asclepiadaceae, species have been defined primarily on discontinuities in floral characters. Vegetative characters provide useful secondary data for specific delimitation or for defining groups of species. However, no study (including the present) has ever really addressed the relative worth of floral characters as opposed to purely vegetative ones for taxon delimitation. Certainly, in terms of the breeding biology of species of *Hoya*, there are some obvious barriers to the insertion of pollinia of a given taxon into the slit between the anther wings of taxa with markedly different flowers. In other cases this is less so. Given our lack of knowledge of the breeding biology of the group, we feel it is prudent to retain the concept of floral discontinuity in defining species and reject Hill's (1988) definition of species on indumentum orientation and geographic origin.

Hence, we consider that the five groups we have defined in the *H. australis* complex are best treated as subspecies of the one species because there is no discontinuity in floral morphology but a marked discontinuity in vegetative morphology. For the taxa so defined, there are also both ecological and geographical separations.

The trend of increasing leaf succulence in plants of the *H. australis* complex is a result of greater development of mesophyll tissue in the leaf (Forster 1990b). This trend may be interpreted as representing an increasing adaptation to seasonal water deficit with a presumed radiation of plants of the complex out of an ancestral rainforest habitat (subsp. *tenuipes*) into ever drier habitats with the extreme being the sandstone escarpments

of Arnhem Land and the Kimberley (subsp. *rupicola*). The possession of succulent leaves and the ability of plants of *H. australis* to tolerate a wide range of light conditions (Adams *et al.* 1988, cf. subsp. *australis* only) enable plants of this complex to occur in a range of different habitats over a wide geographic range in Australia, Papuasia and Melanesia.

The earliest specific name applicable to the group is *Hoya australis* R. Br. ex Traill, and the five groups defined in **Table 1** equate to the following taxa based on our examination either of type collections or descriptions from the literature.

Group 1: *Hoya australis* R. Br. ex Traill; *Hoya dalrympleana* F. Muell.; *Hoya keysii* Bailey; *Hoya pubescens* Reinecke; *Hoya oligotricha* K. Hill subsp. *oligotricha.*

Group 2: *Gymnema recurvifolium* Blume; *Hoya bicarinata* A. Gray; *Hoya papillantha* Schumann; *Hoya lactea* S. Moore; *Hoya oligotricha* subsp. *tenuipes* K. Hill.

Group 3: *Hoya rupicola* K. Hill.

Group 4: *Hoya sanae* Bailey; *Hoya australis* subsp. *sanae* (Bailey) K. Hill.

Group 5: Undescribed taxon.

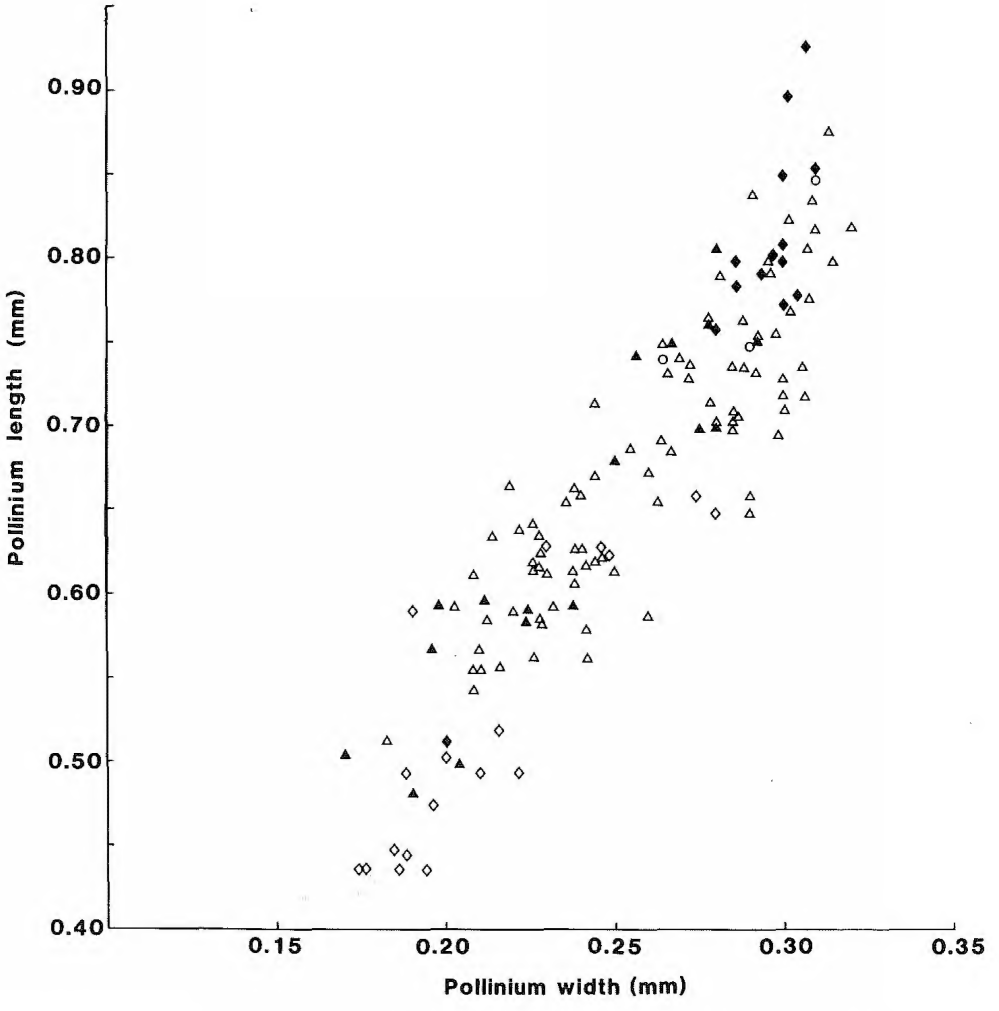

Fig. 3. Pollinium length versus pollinium width in *Hoya australis.* △ Group 1 (subsp. *australis*); ▲ Group 2 (subsp. *sanae*); ◆ Group 3 (subsp. *rupicola*); ◇ Group 4 (subsp. *tenuipes*); ○ Group 5 (subsp. *oramicola.*

Taxonomic Treatment

Hoya australis R.Br. ex Traill, Trans. Hort. Soc. 7: 28 (1830). **Type:** Queensland. COOK DISTRICT: Cape Grafton, [1770] *Banks & Solander* (holo: BM!).

Succulent vine to subshrub. Stems cylindrical, succulent becoming somewhat woody with age; twining or clambering, glabrous or with indumentum when young. Leaves petiolate; lamina succulent, fleshy to coriaceous, elliptic, narrow-ovate, oblong, ovate or orbicular, up to 15 cm long and 12 cm wide, glabrous or with indumentum; tip acuminate, acute or apiculate; base rounded, cordate, obtuse or cuneate; petiole up to 2 cm long; extrafloral nectaries absent or present at lamina base. Cymes racemiform, persistent, with up to 50 flowers; peduncles 1–3 cm long, glabrous or with indumentum. Flowers campanulate 3–5 mm long, 10–25 mm diameter; pedicels 2–4 cm long. Sepals ovate to triangular, 1–5 mm long, 1–3 mm wide, with sparse to dense indumentum and with 1 to several glands at base. Corolla minutely puberulous, white to cream with red under staminal corona; lobes ovate to acute, 5–10 mm long, 3–7 mm wide, apex antrorse, margins revolute. Staminal corona cream; lobes 1.2–3.5 mm long, 1–2.5 mm wide, ovate, concave above, with two longitudinal inrolled keels. Slit between anther wings 0.7–1.2 mm long. Style-head conical, 1–1.5 mm diameter. Ovaries 1.6–2 mm long, 1.4–1.5 mm wide, glabrous. Pollinarium 0.9–1.15 mm long, 0.5–0.8 mm wide; pollinium oblong, 0.56–0.92 mm long, 0.22–0.41 mm wide; corpusculum ovate-oblong, 0.3–0.45 mm long, 0.15–0.24 mm wide; caudicles unwinged, 0.15–0.34 mm long, 0.05–0.14 mm wide. Follicles fusiform 9–13.5 cm long, 1–1.5 cm wide. Seed oblong, tan, 5–7 mm long, 2–3 mm wide; coma 25–30 mm long.

Key to subspecies, based on live or pickled material

1. Margin of leaf lamina strongly recurved 2
   Margin of leaf lamina not recurved 3

2. Leaf lamina <5 cm long, secondary venation prominent . . . . . subsp. **sanae**
   Leaf lamina >5 cm long, secondary venation obscure . . . . . subsp. **oramicola**

3. Plant erect, not twining; leaf lamina very succulent, lacking extrafloral nectaries at base. . . . . subsp. **rupicola**
   Plant twining; leaf lamina coriaceous, fleshy or succulent, with extrafloral nectaries at base 4

4. Foliage with sparse to dense indumentum; leaf lamina fleshy or succulent . . . . . subsp. **australis**
   Foliage glabrous or with sparse indumentum; leaf lamina coriaceous . . . . . subsp. **tenuipes**

1. Hoya australis R. Br. ex Traill subsp. **australis**

Hoya dalrympleana F. Muell., Rep. Burdekin Exped. 16 (1861). **Type:** Queensland. NORTH KENNEDY DISTRICT: On granite hills at Cape Cleveland, *E. Fitzalan* (holo: *n.v.*).

Hoya pilosa Seem., Bonplandia 9: 257 (1861), *nom. nud.* (*fide* A.C. Smith, Fl. Fiji 4: 118 (1988)).

Hoya keysii Bailey, Proc. Roy. Soc. Queensland 1: 87 (1884). **Type:** Queensland. BURNETT DISTRICT: Mount Perry, climbing over rocks, *J. Keys* (holo: BM *n.v.*, photo at BRI!).

Hoya pubescens Reinecke, Bot. Jahrb. Syst. 23: 669 (1898). **Type:** Samoa. Upolu, Apia, Jan 1894, *Reinecke* 220 (holo: B†; iso: BISH!).

Hoya oligotricha K. Hill, Telopea 3: 253 (1988), **synon. nov. Type:** Queensland. COOK DISTRICT: Davies Ck, E of Mareeba, *D. Liddle* (holo: NSW *n.v.*; iso: L *n.v.*, BRI, K not received).

Illustrations: Bailey, Compr. cat. Queensland pl. t. 309, 310 (1913); Jones & Gray, Aust. Climbing Pl. t. 118, 119, 120 (1977); Williams, Native Pl. Queensland 1: 160 (1979); Liddle, Hoya in Australia Fig. 5 (1986); Hill, Telopea 3: 245 (1988).

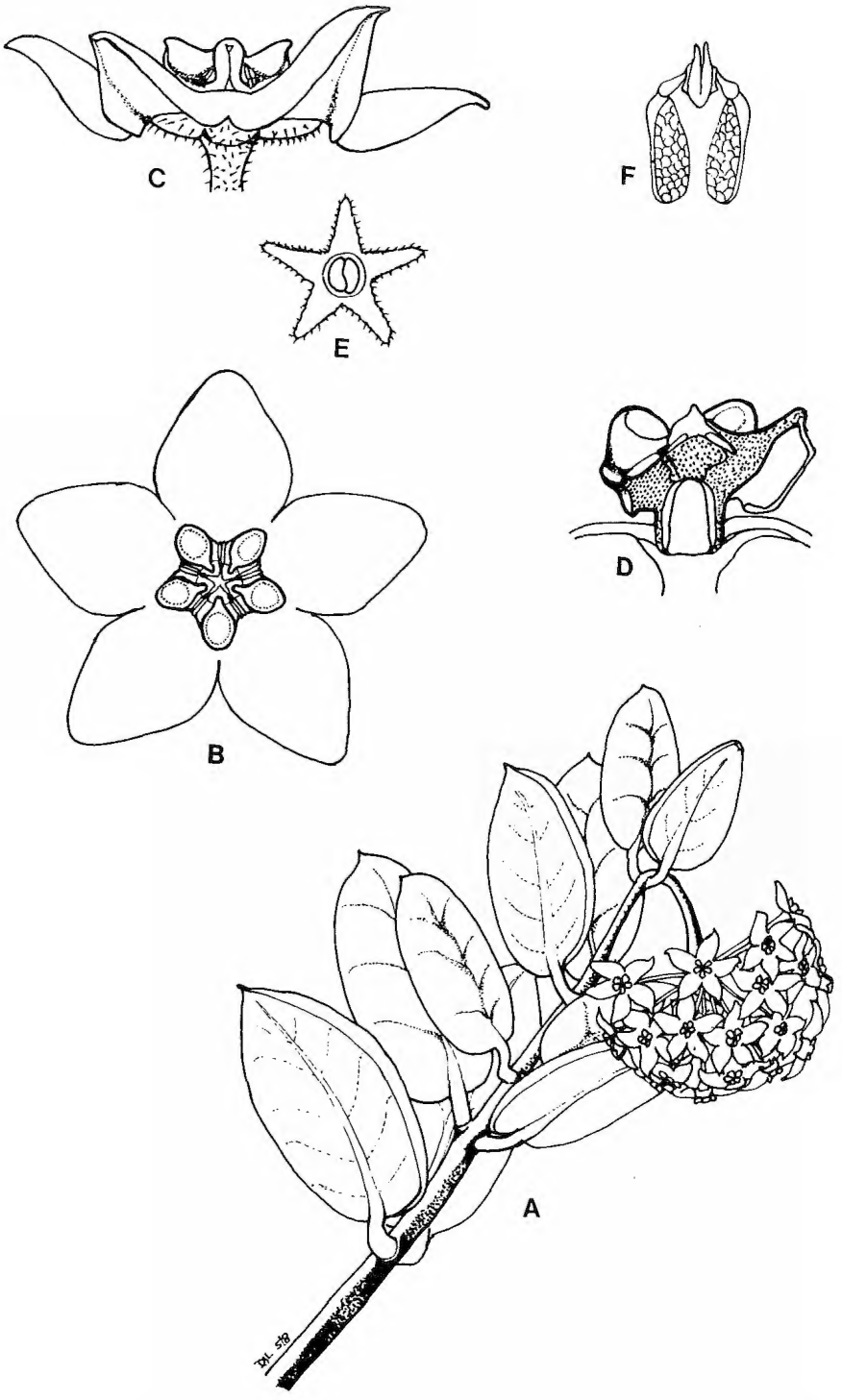

Fig. 4. *Hoya australis* subsp. *australis*: A. habit of flowering plant × 0.5. B. apical view of flower × 3. C. side view of flower × 3. D. vertical cross-section of flower × 6. E. calyx and ovaries from above × 6. F. pollinarium (inverted) × 20. A–F, Liddle IML599. Del. D.J. Liddle.

Vine or rarely a twining subshrub. Foliage with sparse to dense indumentum. Leaf lamina fleshy to succulent, with extrafloral nectaries at base; margins not strongly recurved; secondary venation obscure. **Fig. 4.**

Selected specimens: Australia. Queensland. COOK DISTRICT: Nagir Is, 10°30′S, 142°30′E, Oct 1983, *Liddle* IML288 (BRI); cult. Emerald Ck (ex plant collected Head of Hann Ck, 12°28′S, 142°59′E), Apr 1988, *Lavarack* IML528 (BRI); T.R. 14, Rocky River, 13°50′S, 143°25′E, Sep 1973, *Hyland* 6807 (QRS); Silver Plains, 13°06′S, 143°22′E, Jul 1982, *Liddle* IML208 (BRI); Cape Grafton, 16°52′S, 145°55′E, Jun 1986, *Watts* IML606 (BRI); Davies Ck, 17°03′S, 145°35′E, Apr 1980, *Liddle* IML5 (BRI,MEL,QRS). NORTH KENNEDY DISTRICT: cult. Indooroopilly (ex plant collected by R. Lockyer, 1 mile W of Ravenshoe, Bald Rock Trig Stn, 17°36′S, 145°27′E, Feb. 1986), *Forster* 2383 (BRI). SOUTH KENNEDY DISTRICT: Bailey Islet, May 1969, *Firth* [AQ 007897] (BRI). LEICHHARDT DISTRICT: Rainbow Falls, Blackdown Tableland N.P., 23°51′S, 149°06′E, May 1984, *Forster* 1785 (BRI). PORT CURTIS DISTRICT: Mt Hedlow, 27.5 km N of Rockhampton, 23°07′S, 150°35′E, May 1984, *Forster* 1805 (BRI). BURNETT DISTRICT: 2 km SW of Boolbunda Rock, 25°08′S, 151°41′E, May 1986, *Forster* 2424 (BRI); Mt Lorna, "Toondahra", 42 km SSE of Mundubbera, 25°29′S, 151°21′E, Mar 1984, *Forster* 1755 (BRI). WIDE BAY DISTRICT: Black Gin Ck, T.R. 580, 25°29′S, 151°55′E, May 1987, *Forster* 2906 (BRI). MORETON DISTRICT: Flinton Hill, Worlds End Pocket, Brisbane River, 27°31′S, 152°45′E, Mar 1983, *Forster* 1843 (BRI); Ivorys Rock, 17 km S of Ipswich, 27°46′S, 152°47′E, Aug 1984, *Forster* 1871, *Bostock & Bird* (BRI,MEL). **New South Wales.** cult. Indooroopilly (ex plant collected by N. Skennar from Glenugie Peak, 29°50′S, 152°56′E), Jul 1985, *Forster* 2036 (BRI). **Vanuatu.** Malekula, Tisbel, Sep 1971, *Halle* RSNH6330 (P); Piste de Bunlap, Apr 1977, *Morat* 5489 (P); Aneityum Is, Vtgi, Mar 1939, *Wilson* 1002 (P).

Distribution and habitat: This subspecies occurs in eastern Australia (**Map A**) from Torres Strait south to northern New South Wales and is also in Melanesia (cf. type of *H. pubescens* Reinecke, pubescent forms discussed by Smith (1988) and specimens cited). Plants grow on rock outcrops or cliffs in open eucalypt forest or heath in northern Queensland and in vinethickets and vineforests in southern Queensland, New South Wales and Melanesia. Plants growing on the mainland of Cape York Peninsula north of 12°28′S are mostly subsp. *sanae* (Bailey) K. Hill.

Phenology: Australian populations flower from March to May and fruit 3–4 months later.

Notes: As noted by Henderson (1983), *H. australis* had a rather informal entry into the taxonomic literature, with the result that the correct author citation and place of publication has often been confused, particularly in the horticultural literature. Brown (1810) listed Australian material of *Hoya* under *H. carnosa* which is an Asian species, with the comment that the material could well be specifically distinct. In the Prodromus, Brown listed the locality for Australian *Hoya* as (T) and said that he had seen plants of it living (v.v.), thus indicating that material he worked with was collected by him somewhere on the coast of Queensland and the Northern Territory westward to Arnhem Bay (Stearn 1960). The first effective publication of *H. australis* is that of Traill (1830) who stated "The first is a native of the more northern part of New South Wales, with leaves varying from elliptic to obovate; this is in the Herbarium of Mr. Robert Brown, and is named by him Hoya australis, it having been referred by him in his Prodromus Flora Novae Hollandiae, Vol. i. page 460, with a doubt, to H. carnosa."

No material of *H. australis* exists at BM that was collected by Brown. A Banks and Solander collection from Cape Grafton near Cairns is present in BM and is the material illustrated in Banks and Solander (1901). There are two sheets of this, one (the poorer) which was taken by Brown on the voyage with Flinders, and the other which has written in Brown's handwriting – *H. australis*. This latter sheet is undoubtedly that seen by Traill and is the type of *H. australis*. Brown's omission of "B" from the relevant text in the Prodromus, indicating use of Banks and Solander material (Burbidge 1955; Stearn 1960) is apparently an error.

Recollection of material both at Cape Grafton and adjoining areas revealed plants with variable leaf form, but all consistently with small (<10 cm long and 5 cm wide), orbicular, densely pubescent succulent leaves. *Watts* IML600 from Rocky Island off Cape Grafton, in particular is similar to that illustrated by Banks and Solander (1901).

We have been unable to locate the type of *H. dalrympleana* which is apparently not at MEL (H. Aston, pers. comm. 1990) as thought by Hill (1988). We have included it within the synonymy of *H. australis* subsp. *australis* as neither subsp. *tenuipes* nor subsp. *sanae* occurs as far south as Townsville.

The isotype of *H. pubescens* at BISH is poor but both the stems and petioles have a sparse to dense indumentum. As outlined by Smith (1988), such pubescent plants are

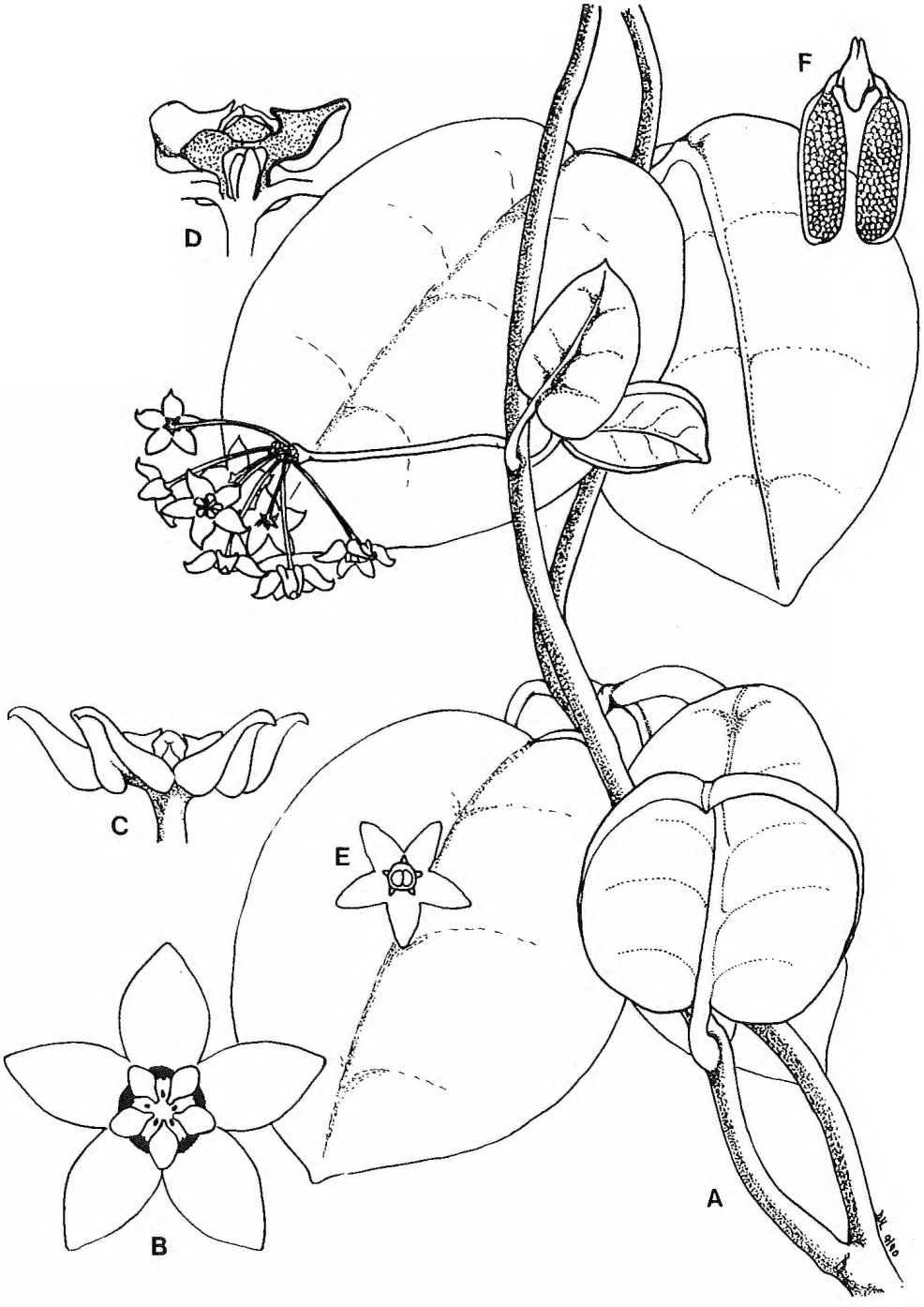

Fig. 5. *Hoya australis* subsp. *tenuipes*: A. habit of flowering plant × 0.5. B. apical view of flower × 2.5. C. side view of flower × 2.5. D. vertical cross-section of flower × 5. E. calyx and ovaries from above × 2.5. F. pollinarium (inverted) × 25. A–F, Liddle IML1. Del. D.J. Liddle.

relatively common in parts of Melanesia and from the specimens we have examined, this subspecies occurs both in Samoa and Vanuatu.

The type of *H. keysii* is not at BRI as was previously thought (Hill 1988: 250), but at BM (Forster 1989). This is an unusual location for an F.M. Bailey holotype; BM should be considered when seeking location of missing types relative to other taxa described by him. Small densely pubescent, orbicular-leaved plants that are more or less identical with the type of *H. keysii* were relocated at Boolbunda Rock near Mt Perry (*Forster* 2424). These plants are very similar to those from Cape Grafton.

Plants at Davies Creek, the type locality of *H. oligotricha*, are virtually indistinguishable from the Cape Grafton plants, so the recognition of *H. oligotricha* in addition to *H. australis* by Hill (1988) is unnecessary. One of us originally collected the material at Davies Ck from which Hill purportedly prepared his type material, however we have not seen the resultant herbarium specimens and this type material does not appear to have been distributed, at least to BRI and K. In addition to the type collection of *H. oligotricha*, Hill cites a different collection from Davies Creek for *H. australis sensu* Hill. Both of these collections are referable to *H. australis* subsp. *australis*. Apart from indumentum development on the lamina, the main criterion by which *H. oligotricha* subsp. *oligotricha* is distinguished by Hill from *H. australis* subsp. *australis*, is that in southern Queensland it is a coastal plant whereas the other species is "restricted to the ranges". While we do not wish to belabour this misconception, many populations can be found where there is no distinction. As examples, *Kenning* IML566 from Lake Bowraddy on Fraser Island ("a coastal sand habitat") is quite pubescent, and *Forster* 4275 from the top of Mt Perry ("the ranges") is almost glabrous.

Conservation status: This is a very common plant and is not endangered. Plants are widely cultivated under a variety of names, sometimes even correctly as *H. australis*!

2. Hoya australis subsp. **tenuipes** (K. Hill) P. Forster & D. Liddle, **comb. nov.** *Hoya oligotricha* subsp. *tenuipes* K. Hill, Telopea 3: 254 (1988). **Type:** Queensland, COOK DISTRICT: Pascoe River Rockpile, 16 September 1978, *B. Wallace* 83252 (holo: NSW *n.v.*; iso: L *n.v.*; BRI,K not received).

Gymnema recurvifolium Blume, Mus. Bot. 1: 150 (1850), **synon. nov. Type:** Nov. Guinea, *Zippelius* (holo: [L898168-39, L898168-41] L!).

Hoya bicarinata A. Gray, Proc. Am. Acad. Arts Sc. 5: 335 (1862). **Type:** Tonga. Tongatapu, *U.S. Expl. Exped.* [US78372] (lecto: US!; *fide* A.C. Smith, Fl. Fiji 4: 118 (1988)).

Hoya barrackii Horne, A Year in Fiji (1881), nom. nud. (*fide* A.C. Smith, Fl. Fiji 4: 118 (1988)).

Hoya papillantha Schumann, Notizbl. Bot. Gart. Mus. Berl. 2: 142 (1898), **synon. nov. Type:** "Neu-Lanenburg-Gruppe, Credner-Insel, an einem Stamme vou subcordata", Jul 1896, *Dahl* 239 (holo: B†).

Hoya lactea S. Moore, J. Bot. 52: 293 (1911), **synon. nov. Type:** Papua New Guinea. CENTRAL PROVINCE: Mt Gandada, *H.O. Forbes* 872 (syn: BM *n.v.*, photo at BRI!); without locality, *H.O. Forbes* 925 (syn: BM *n.v.*).
Illustration: Liddle, Hoya in Australia Figs 10 & 11 (1986).

Vine. Foliage glabrous or with scattered to sparse indumentum. Leaf lamina coriaceous, with extrafloral nectaries at base; margins not strongly recurved; secondary venation obscure. **Fig. 5.**

Selected specimens: Irian Jaya. Warnapi, 15 km N of Ransiki, Vogelkop, Sep 1948, *Kostermans* 2715 (L); Cycloop Mtns, road Hollandia – Sentani, Jun 1961, *van Royen & Sleumer* 5715 (BRI,L). **Papua New Guinea.** MADANG PROVINCE: Josephstaal, 4°45′S, 145°00′E, Sep 1958, *White* [NGF10323] (A,BRI,CANB). NEW BRITAIN: Bei Massawa, Nov 1901, *Schlechter* 13707 (WRSL). BOUGAINVILLE: Arawa Plantation, 6°15′S, 155°40′E, Dec 1960, *Millar* [NGF38401] (BRI,CANB,L). SOUTHERN HIGHLANDS PROVINCE: Near Moro, Lake Kutubu, 6°22′S, 143°14′E, Oct 1961, *Schodde* 2445 (A,CANB,L). MOROBE PROVINCE: track to Mt Shungol, 6°50′S, 146°45′E, Nov 1970, *Stevens* [LAE50489] (A,BRI,CANB,L). NORTHERN PROVINCE: Near Ridubidubina camp, Aug 1954, *Hoogland* 4509 (A, L). WESTERN PROVINCE: Daru Is, 9°07′S, 143°20′E, Aug 1967, *Ridsdale* [NGF33759] (L). CENTRAL PROVINCE: Boridi, Nov 1935, *Carr* 13467 (CANB,L). MILNE BAY PROVINCE: Biniguni, Mayu I track, 9°38′S, 149°18′E, Jun 1972, *Streimann & Leach* [NGF28579] (BRI,CANB). **Solomon Islands.** San Cristobal, mouth of Muni River, Aug 1965, *Sore* 2331 (A,L). **Australia. Queensland.** COOK DISTRICT: Mulingar, McIlwraith Range, Apr 1979, *Liddle* IML25 (BRI); Lankelly Ck, 13°53′S, 143°18′E, Apr 1979, *Liddle* IML26, IML27 (BRI); Daintree Barge, 16°17′S, 145°24′E, Aug 1979, *Liddle* IML3 (BRI); Atherton, 16°34′S, 145°40′E, Apr 1978, *Liddle* IML1 (BRI). NORTH

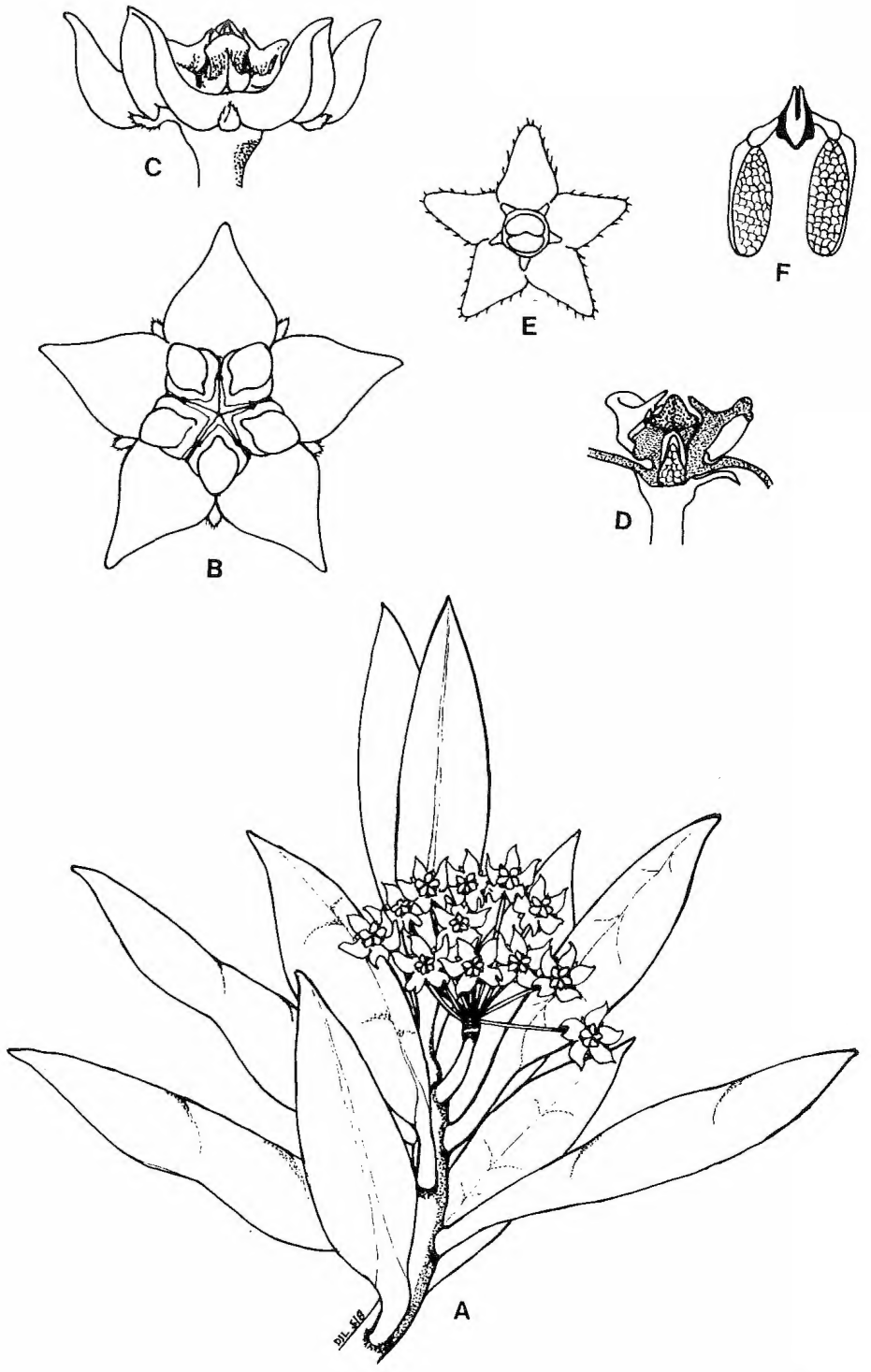

Fig. 6. *Hoya australis* subsp. *rupicola*: A. habit of flowering plant × 0.5. B. apical view of flower × 3. C. side view of flower × 3. D. vertical cross-section of flower × 3. E. apical view of calyx and ovaries × 3. F. pollinarium (inverted) × 20. A–F, Liddle IML758. Del. D.J. Liddle.

KENNEDY DISTRICT: cult. Indooroopilly (ex plant collected by R. Lockyer at Charmillan Ck, c. 12 km SSW of Ravenshoe, 17°42′S, 145°31′E, Feb 1986), *Forster* 2380 (BRI). **New Caledonia.** Paita, Mont Lulu, Ile Wallis, Dec 1981, *McKee* 40077 (P). **Fiji.** Vitu Levu, Sep 1947, *Smith* 6256 (BRI); cult. Indooroopilly (ex plant collected by P. Spence on Mana Is), Apr 1986, *Forster* 2394 (BRI).

Distribution and habitat: This subspecies occurs in Queensland (**Map B**) on southern Cape York Peninsula south to Innisfail and also in New Guinea, the Solomon Islands and Melanesia. Plants grow in rainforests, vineforests or adjacent to mangroves either as epiphytes or lithophytes.

Phenology: In Australia, the main flowering period is from September to October, although there may be a few flowers present in April or May; fruits appear 3–4 months later.

Notes: The most distinctive features of this subspecies are the more or less glabrous, coriaceous to fleshy foliage, and the slender peduncles. Both characters were recognised by Hill so that our concept of this taxon is similar to his. We consider the taxon also occurs in New Guinea and Melanesia where it has been previously described several times at the specific level. An excellent account of the taxa of this complex of Hoyas described from Melanesia including notes on typification, nomenclature and indumentum development, is given by Smith (1988). In this, subspecies *tenuipes* appears to be the most frequently collected taxon in that region.

The type collection of *Gymnema recurvifolium* which comprises two sheets, has inflorescences with only very young buds present. Dissection of some of those buds was not particularly informative as to the generic placement of the material as neither the staminal column nor pollinaria were developed. On the basis of the foliage and racemiform, persistent peduncles this material does not belong to *Gymnema* (soon to be included in *Marsdenia* R. Br. or *Stephanotis* Thouars (cf. Forster 1990a)) and is not referable to any taxon of *Marsdenia* s.l. that occurs in Papuasia (Forster unpubl.). This material is, however, an excellent vegetative match for other collections of *H. australis* subsp. *tenuipes* from Papuasia so we are confident on the inclusion of Blume's taxon within this subspecies.

The lectotype of *H. bicarinata* at US is rather fragmentary. It has glabrous upper leaf surfaces and on the lower leaf surface is glabrous except for scattered indumentum on the midrib.

The type of *H. papillantha* is not extant. However, we have been able to locate a specimen (*Schlechter* 13707) subsequently cited under this name by Schlechter (1905) who compared his material with the type in B. This collection is glabrous and typical of the coriaceous large-leaved plants that have been collected from New Britain, Bougainville and the Solomon Islands.

Conservation status: This subspecies is commonly encountered and is not endangered. Plants are widely cultivated.

3. Hoya australis subsp. **rupicola** (K. Hill) P. Forster & D. Liddle, **comb. et stat. nov.**
Hoya rupicola K. Hill, Telopea 3: 252 (1988). **Type:** Northern Territory. Deaf Adder Gorge, 24 February 1977, *R.E. Fox* 2548 (holo: NSW *n.v.*; iso: CANB!,DNA!).

Subshrub or trailer, not climbing. Foliage with dense indumentum. Leaf lamina very succulent, lacking extrafloral nectaries at base; margins not strongly recurved; secondary venation obscure. **Fig. 6.**

Selected specimens: Western Australia. Surveyors Pool, Mitchell Plateau, 14°41′S, 125°43′E, Jun 1976, *Kenneally* 5075 (PERTH); Camp Ck, Mitchell Plateau, 14°53′S, 125°44′E, Jan 1982, *Kenneally* 7788 (PERTH); Summit of Mt Trafalgar, Prince Regent River Reserve, 15°17′S, 125°04′E, Aug 1974, *George* 12800 (PERTH); Fern Gully, Garipeli Ck, Prince Regent River Reserve, 15°32′S, 125°13′E, Aug 1974, *George* 12639 (BRI,PERTH). **Northern Territory.** Wessel Is., 11°11′S, 136°44′E, Oct 1972, *Latz* 3356 (AD,BRI,DNA); Stevens Is, The Wessels, 11°34′S, 136°06′E, Dec 1987, *Russell-Smith* 4527 & *Lucas* (DNA); On rocks near the Giddy River, 12°22′S, 136°42′E, *Symon* 7870 (CANB); cult. Emerald Ck (ex plant collected at Obiri Rock, East Alligator River Crossing, 12°23′S, 132°56′E), *Liddle* IML623 (BRI); East Alligator River area, near Mt Howship, Arnhem Land, 12°35′S, 133°10′E, Feb 1984, *Jones* 1461 (CANB,DNA); Buffalo Springs, Mt Brockman, 5 km NE of Koongarra, 12°50′S, 132°53′E, May 1980, *Lazarides* 8912 (CANB); Badalngarrmirri Ck, Arnhem Land, 12°53′S, 135°50′E, Sep 1985, *Weightman* 2227 (CANB,DNA); 2 miles W of old BHP airstrip, 12°54′S, 135°28′E, *Symon* 7737 (AD,DNA,PERTH); Florence Falls, Tabletop Range, 13°06′S, 130°46′E, May 1985, *Dunlop* 6815 (BRI,DNA); top of Wangi Falls, 13°11′S, 130°49′E, Aug 1986, *Smith* 52 (DNA); Tabletop Range, 13°13′S, 130°43′E, Nov 1989, *Forster* 6077 (BRI); Barrk Malam walk, Jim Jim Falls, 13°16′S, 132°50′E, Dec 1989, *Forster* 6126 (BRI); Edith River, 14°09′S, 132°16′E, Sep 1974, *Dunlop* 3644 (DNA); Ruined City, 50 km NNE of Ngukurr, 14°17′S, 134°55′E, Nov 1987, *Russell-*

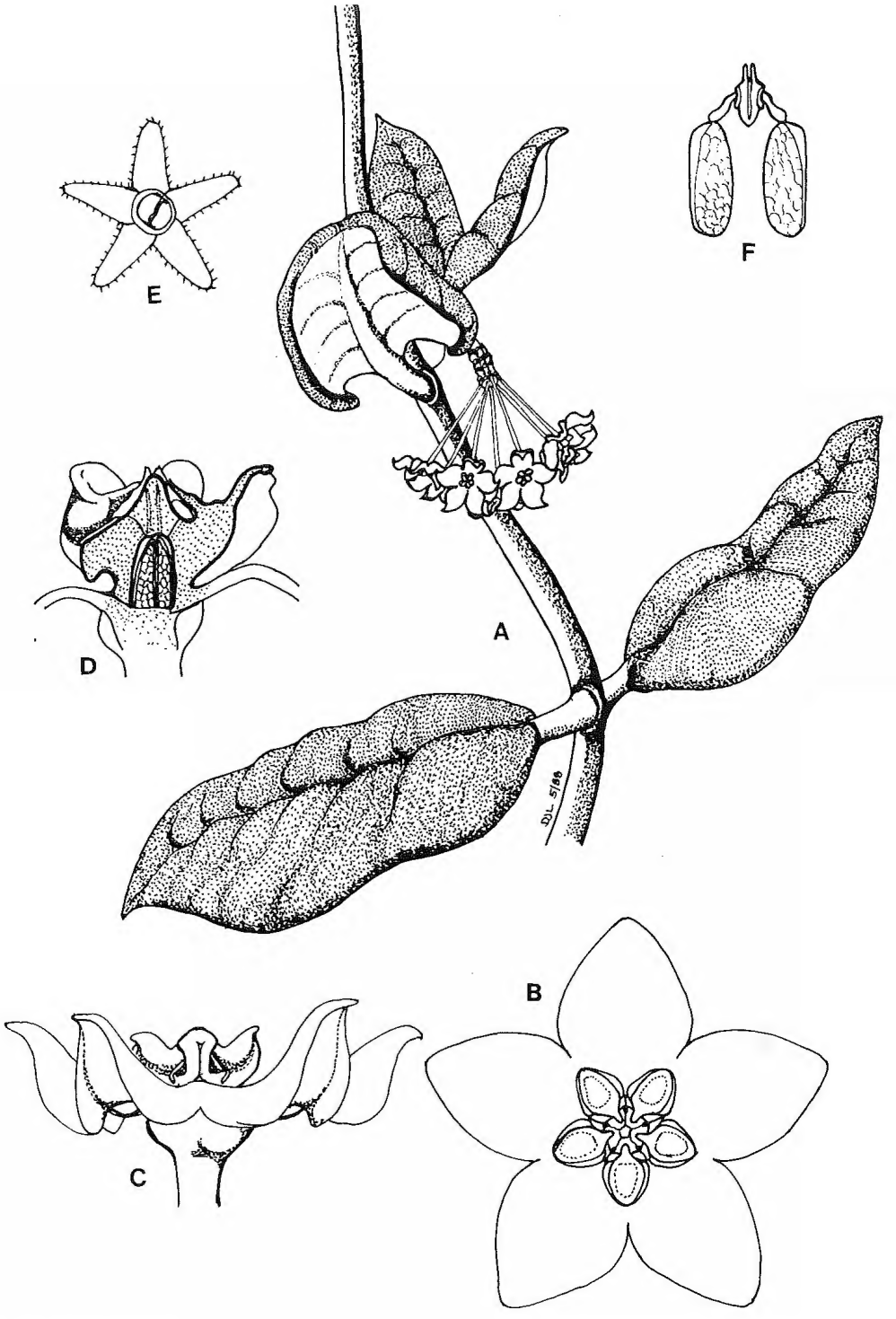

Fig. 7. *Hoya australis* subsp. *oramicola*: A. habit of flowering plant × 0.5. B. apical view of flower × 3. C. side view of flower × 3. D. vertical cross-section of flower × 6. E. apical view of calyx and ovaries × 3. F. pollinarium (inverted) × 20. A–F, Liddle IML123. Del. D.J. Liddle.

Smith 4190 & *Lucas* (DNA); Katherine Gorge N.P., 14°18′S, 132°28′E, Apr 1968, *Byrnes* 623 (DNA); Macadam Range, 14°41′S, 129°44′E, Mar 1989, *Russell-Smith* 7456b & *Lucas* (DNA).

Distribution and habitat: This subspecies occurs in the Kimberley region of Western Australia and over much of the top end of the Northern Territory (**Map A**). Plants grow on sandstone outcrops and cliffs.

Phenology: Flowers January to March; fruits 3–4 months later.

Conservation status: This subspecies is commonly encountered throughout its range and is not endangered. It is represented in a large number of conservation reserves such as Litchfield Conservation Park and Katherine and Kakadu National Parks in the Northern Territory.

Notes: This subspecies generally occurs as an erect subshrub although this would appear to be a result of the exposed habitats in which it normally occurs. For example at Jim Jim Falls, Northern Territory, the plants may cascade down rock faces for up to 20 m. Subspecies *rupicola* is distinctive within *H. australis* in that it is the only subspecies that does not twine, but throws out long runners that may clamber over surrounding rocks and vegetation. Leaves are very succulent and this may be interpreted as an adaptation to the marked monsoon environment in which it occurs.

While subsp. *rupicola* is a very distinctive plant, particularly as regards habit and the very succulent leaves, this distinctiveness is lessened by the recognition of subsp. *oramicola* as a link between subsp. *rupicola* and the other subspecies. While flowers in the majority of populations of subsp. *rupicola* do have large calyces (cf. Hill 1988), several (*George* 12639 and *Liddle* IML623) do not so this attribute cannot be used effectively as a diagnostic character.

4. Hoya australis subsp. **oramicola** P. Forster & D. Liddle **subsp. nov.** ab subsp. *australi* foliis ad basin laminae nectaria extrafloralia carentibus, maginibus laminae valde recurvis differt. **Typus:** Northern Territory. 7 km NE Lubra Point, Bathurst Island, 1 July 1988, *J. Russell-Smith* 5812 & *D. Lucas* (holo: DNA!).

Vine. Foliage with sparse to dense indumentum. Leaf lamina succulent, lacking extrafloral nectaries at base, greater than 5 cm long; margins strongly recurved; secondary venation obscure. **Fig. 7.**

Specimens examined: Northern Territory. Conder Point, Melville Island, *Russell-Smith* 2410 & *Lucas* (DNA); ditto, Nov 1989, *Forster* 6086 & *Russell-Smith* (BRI); cult. Emerald Ck (ex plant putatively from Talc Head, Darwin area), Feb 1988, *Liddle* IML424 (BRI); cult. Emerald Ck (ex plant putatively from Mandorah, Darwin area), Feb 1988, *Liddle* IML123 (BRI).

Distribution and habitat: This subspecies is apparently restricted to Melville and Bathurst Islands north of Darwin in the Northern Territory (**Map B**). Material in cultivation is labelled as Talc Head and Mandorah, both localities near Darwin. We have not been able to relocate plants at these localities. Plants grow as canopy lianes in monsoon vine thicket on red laterite on Melville and Bathurst Islands.

Phenology: Flowers July; fruits 3–4 months later.

Notes: This subspecies appears to be intermediate between subsp. *rupicola*, which does not twine and occurs on sandstone, and the twining subsp. *sanae*, which occurs in vine thickets on sand-dunes.

Conservation status: This subspecies has been rarely collected and the small populations on Melville and Bathurst Islands should be monitored and conserved.

5. Hoya australis subsp. **sanae** (Bailey) K. Hill, Telopea 3: 251 (1988); *Hoya sanae* Bailey, Queensland Agric. J. 1: 229 (1897) ("sana"). **Type:** Queensland. COOK DISTRICT: Polo Creek, Somerset, *F.L. Jardine* (holo: BRI!).
Illustrations: Bailey, Compr. cat. Queensland pl. t. 308 (1913); Liddle, Hoya in Australia Figs 8 & 9 (1986).

Vine. Foliage with sparse to dense indumentum. Leaf lamina succulent, less than 5 cm long, usually lacking extrafloral nectaries at base, but occasionally present; margins strongly recurved; secondary venation prominent. **Fig. 8.**

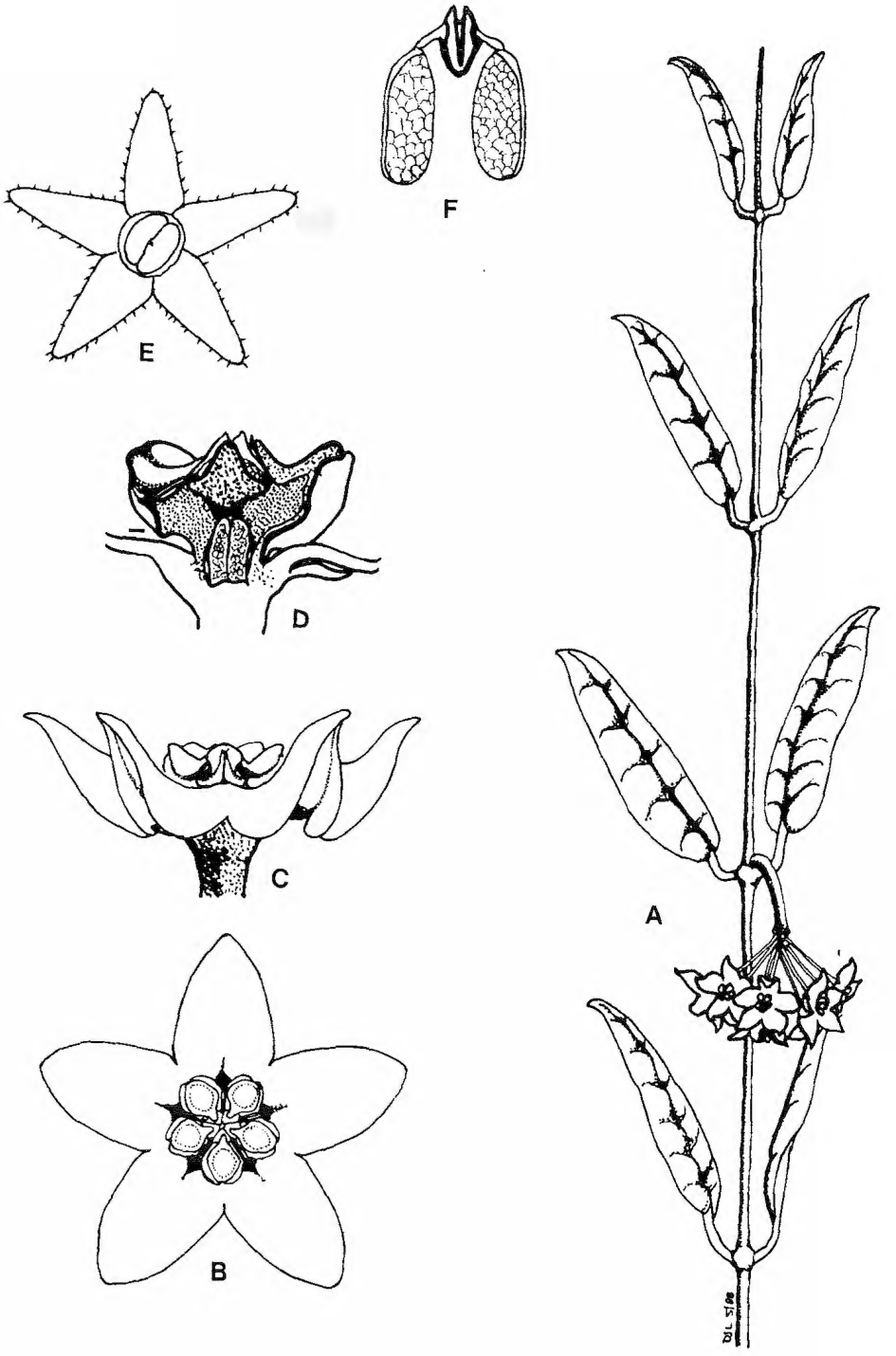

Fig. 8. *Hoya australis* subsp. *sanae*. A, habit of flowering plant × 0.5. B, apical view of flower × 2.5. C, side view of flower × 2.5. D, vertical cross-section of flower × 5. E, apical view of calyx and ovaries × 5. F, pollinarium (inverted) × 20. A–F, Liddle IML171a. Del. D.J. Liddle.

Selected specimens: Australia. Queensland. COOK DISTRICT: Badu Is, Torres Strait, 10°07′S, 142°09′E, Jul 1979, *Garnett* 132 (BRI); Banks (Moa) Is, Torres Strait, 10°10′S, 142°15′E, Feb 1975, *Cameron* 20582 (QRS); c. 2 km S of Cape York, 10°43′S, 142°32′E, Jun 1988, *Forster & Liddle* 4436, 4437 (BRI); Ida Is, Torres Strait, 10°43′S, 142°34′E, Oct 1983, *Liddle* IML289 (BRI); 1 km S of Punsand Bay, 10°44′S, 142°29′E, Jun 1988, *Forster & Liddle* 4439 (BRI); Newcastle Bay, 2.5 miles S of Somerset, *Brass* 18771 (BRI,CANB); Newcastle Bay, headland between Narau & Nanthau beaches, 10°47′S, 142°35′E, Feb 1990, *Forster* 6381 (BRI); 1 km E of Muttee Head, 10°55′S, 142°15′E, Jun 1988, *Forster & Liddle* 4474 (BRI); Muttee Head, 10°56′S, 142°17′E, Apr 1982, *Liddle* IML171a,b (BRI); Tributary of Escape River, *Clarkson* 2083 (BRI); cult. Emerald Creek (ex plant collected at Captain Billy Ck, 11°38′S, 142°51′E), May 1988, *Collins* IML31 (BRI); Olive River, 12°10′S, 143°05′E, Sep 1974, *Hyland* 7497 (BRI,QRS); Turtle Bay, Jul 1943, *Blake* 14973 (BRI); c. 1 km along road to Bolt Head, off road from Maloneys Springs, 12°28′S, 143°01′E, Jun 1989, *Forster & Liddle* 5525 (BRI).

Distribution and habitat: This subspecies occurs on Cape York Peninsula, Queensland and several offshore islands (**Map B**). Plants grow in foreshore monsoon vine thickets on white sand.

Phenology: Flowers May-June; fruits 3–4 months later.

Notes: As with subsp. *oramicola* the most distinctive features of subsp. *sanae* are the strongly recurved margins of the leaf lamina that may almost touch one another when the leaves are strongly desiccated during the dry season. This feature is not particularly noticeable on dried material and may explain why Hill did not comment on this characteristic in his account. Although Hill stated that "zones of intergradation [of this subspecies] with subsp. *australis* occur around Cooktown and somewhat south of there" our field studies showed that the populations from Silver Plains and Silver Valley are referable to subsp. *australis*.

Bailey originally spelt the epithet as "sana" but as the taxon was named for Mrs Sana Jardine, the correct spelling of the epithet is "sanae".

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A large number of people and some institutions have aided this revision in the collection or provision of live material and we would like to thank E. Anderson; Australian National Botanic Gardens, Canberra; G. Batianoff; L. Bird; P. Bostock; D. Brewer; J. Clarkson; R. Collins; J. Conran; A. Cribb; D. Cumming; G. Defina; R. Dowling; G. & A. England; B. Ghen; B. Gray; K. Halfpapp; G. Hardy; R. Harvey; H. Hepburn; M. Hodge; B. Hyland; K. Kenneally; G. Kenning; P. Lavarack; R. Lockyer; R. McIllwain; M. O'Brien; M. Olsen; Mount Coot-tha Botanic Gardens; D. Orford; G. Sankowsky, V. Scarth-Johnson; P. Sharpe; M. Smith; J. Russell-Smith & D. Lucas; M. Telfer; M. Thorsborne; M. Tucker; V. Watts, K. Williams and the various landholders from whose property plants were obtained. The Directors/Curators of A, B, BISH, BM, BRI, CANB, CBG, DNA, JCT, K, L, MEL, QRS, P, PERTH and US provided access to material, either on loan or at their institutions. Staff at the Queensland Herbarium organised and processed loan material. The Queensland National Parks and Wildlife Service and the Queensland Forest Service provided various permits to collect material in areas under their jurisdiction. The Australian Biological Resources Study provided funding to P.I. Forster during 1988 to 1990. All of this assistance is gratefully ackowledged.

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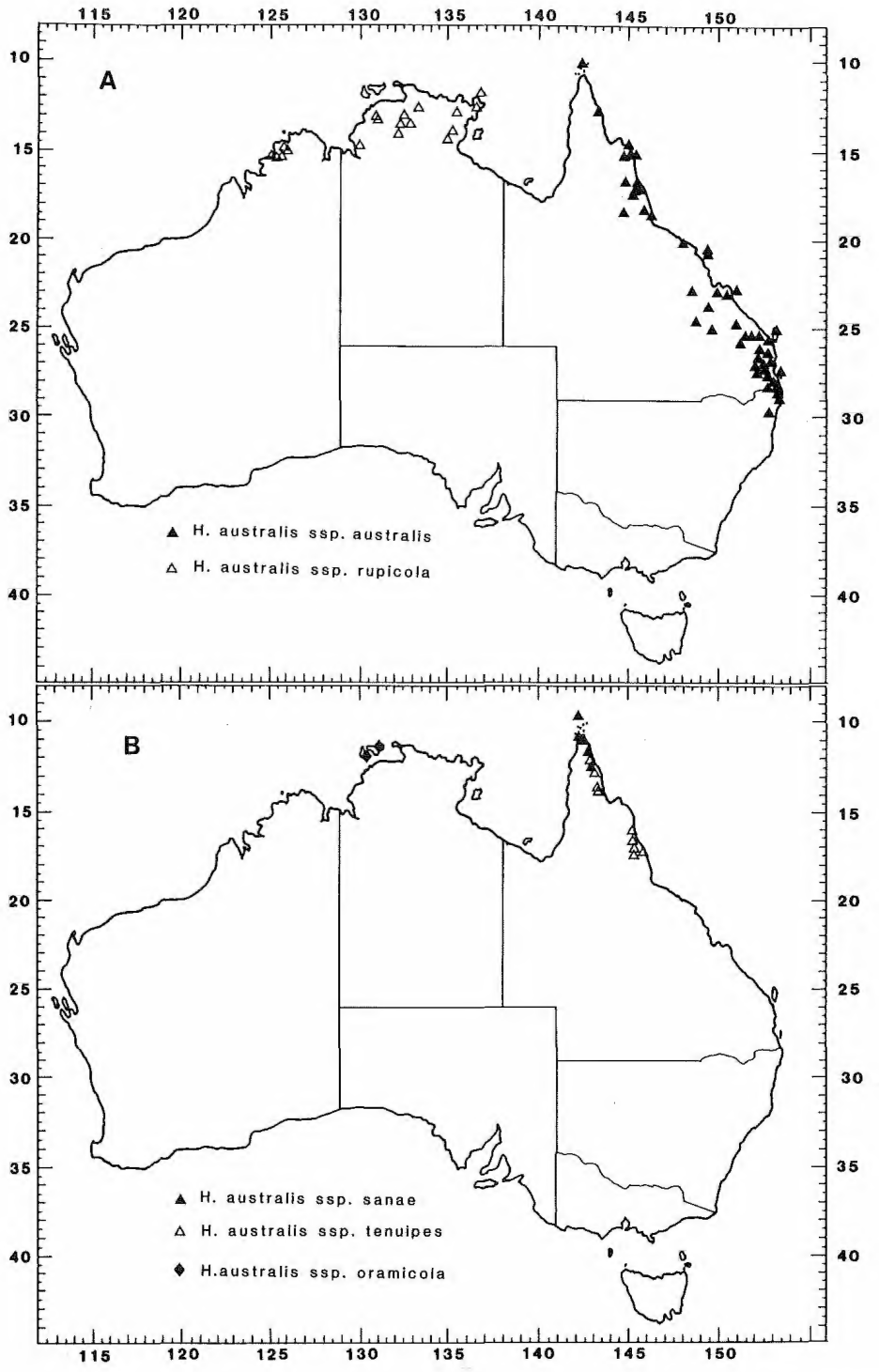

Maps A & B. Distribution of *Hoya australis* in Australia. A. ▲ subsp. *australis*; △ subsp. *rupicola*. B. ▲ subsp. *sanae*; △ subsp. *tenuipes*; ◆ subsp. *oramicola*.

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Appendix 1. Index to numbered collections of *Hoya australis* examined, based on holdings at BRI, CANB, DNA, JCT, PERTH, QRS and partial holdings at A, BISH and L.

1a. *H. australis* subsp. *australis*

1b. *H. australis* subsp. *oramicola*

1c. *H. australis* subsp. *rupicola*

1d. *H. australis* subsp. *sanae*

1e. *H. australis* subsp. *tenuipes*

Note: Individual collectors in the NGF/LAE series are not named.

Adams 935:1c.

Barlow 355:1a; Batianoff & McDonald 222:1a, 568:1a, 688:1a, 1271:1e; Blake 4744:1a, 11287:1a, 14973:1d, 15280:1a, 15392: 1a, 15821: 1a, 21705:1a; Brass 2509:1a, 18771:1d, 25953:1e, 32545:1e; BSIP3934:1e; Byrnes 623:1c, 2485:1c.

Cameron 2573:1d, 20582:1d; Carr 13467:1e; L.E.Cheesman 50:1e; Clarkson 2083: 1d; Collins IML31:1d; Craven 8235:1c; Craven & Schodde 1459:1a.

Dillewaard & Olsen 276:1a; Dockrill & Stevens 374:1a; Dunlop 3644:1c, 5696:1c, 6815:1c.

Feuilletau de Bruyn 121:1e; Fitzsimon 189:1e; Forster 732:1a, 1543:1a, 1656:1a, 1755:1a, 1771:1a, 1783:1a, 1785:1a, 1792:1a, 1795:1a, 1805:1a, 1845:1a, 1851:1a, 1852:1a, 1853:1a, 1856:1a, 1857:1a, 1859:1a, 1883:1a, 1974:1a, 2002:1a, 2005:1a, 2036:1a, 2047:1a, 2070:1a, 2137:1a, 2171:1d, 2265:1a, 2271:1e, 2272:1a, 2274:1a, 2317:1a, 2330:1a, 2332: 1a, 2333:1a, 2335:1a, 2375:1a, 2377:1a, 2380:1e, 2382:1e, 2383:1a, 2394:1e, 2398:1a, 2418:1a, 2424:1a, 2499:1a, 2575:1a, 2655:1a, 2721:1a, 2722:1a, 2906:1a, 2962:1a, 3964:1a, 4275:1a, 6074:1c, 6077:1c, 6079:1c, 6080:1c, 6086:1b, 6381: 1d; Forster & Bird 1854:1a, 2153:1a, 2328:1a, 2881:1a; Forster & Bostock 2052:1a, 2066:1a; Forster & Hoy 5000:1a; Forster & Liddle 4436:1d, 4437:1d, 4439:1d, 4474:1d, 5525:1d; Forster & Russell-Smith 6086:1b; Forster & Telfer 1566:1a, 1569:1a; Forster *et al.* 1860:1a, 1868:1a, 1871:1a, 2071:1a, 2077:1a; Fox 2548:1c; Fryxell, Craven & Stewart 4734:1c;

Gardner 1394: 1c; Garnett 132:1d; George 12639:1c, 12800:1c; Gray 803:1e, 804:1e, 1648:1e, 2036:1d, 4373:1e.

Halfpapp IML486:1e, IML610:1a; Halle RSNH6330:1a; Hartley 10757:1e, 10862:1e; Hearne 142:1c; Henderson *et al.* 840:1a; Heyligers 1054:1a; Hodge IML35:1a; Hoogland 4509:1e, 5188:1e, 9000:1e; Hyland 6708:1a, 6807:1a, 7497:1d, 8875:1e, 9428:1e.

D. Jones 1461:1c; W. Jones 1471:1e, 2537:1d, 2951:1a.

Kanis 1101:1a; Kenneally 2188:1c, 4805:1c, 5075:1c, 7788:1c, 7907:1c; Kenning IML532:1a, IML566:1a; Kostermans 2715: 1e.

Latz 3356:1c; Lavarack IML385:1a, IML528:1a; Lazarides 8912:1c; Liddle IML series, 1:1e, 2:1e, 3:1e, 4:1e, 5:1a, 6:1a, 7:1a, 8:1a, 25:1e, 26:1e, 27:1e, 28:1e, 33:1e, 34:1e, 38:1e, 119:1a, 124:1b, 157:1c, 164:1a, 171a,b:1d, 173:1d, 206:1a, 208:1a, 210:1a, 257:1a, 264:1a, 277:1e, 288:1a, 289:1d, 367:1a, 384:1e, 424:1b, 441:1a, 442:1a, 599:1a, 600:1a, 603:1a, 606:1a, 615:1e, 623:1c, 758:1d, 760:1d.

Mackenzie 710307-8:1c; McDonald & Batianoff 1619A:1a; McKee 9335:1a, 40077:1e; Morat 5489:1a; Moriarty 494:1a; Must 959:1c.

Neldner 820:1a; NGF & LAE series, 9968:1e, 9984:1e, 10323:1e, 14044:1a, 18753:1e, 22744:1e, 26932:1e, 27876:1e, 28579:1e, 33759:1e, 35199:1e, 35650:1e, 36718:1a, 38401:1e, 38486:1e, 40533:1e, 50489:1e, 77254:1e.

O'Brien IML366:1a.

Paijmans 481:1e; Pullen 8158:1e.

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